NEW YORK ENTOMOLOGICAL SOCIETY
LXXXVII(1), 1979, pp. 91–94

POSSIBLE PHYLOGENETIC SIGNIFICANCE OF COMPLEX HAIRS IN BEES AND ANTS

U. N. Lanham

Abstract.—If both larval and adult stages are taken into account, then ants and bees are the only major groups of aculeate Hymenoptera in which complex hairs are abundant. The possible phylogenetic significance of this is discussed.

The first serious attempt at constructing a phylogeny of the higher aculeate Hymenoptera was that of Börner (1919). In it he grouped the bees, scolioid wasps, and ants in a category (the Haplocnemata) which is contrasted with the vespid, pompilid, and sphecid wasps (Diplocnemata). This scheme has been discussed and rejected by Bischoff (p. 546) and Malyshev (p. 255). The modern conception is that the Apoidea are little modified descendants of the Sphecidae, so closely related that both can be included in a single superfamily (Bohart & Menke, p. 31). Börner, however, has made a considerable contribution to the array of characters available to discriminate higher categories, among them the strigil of the hind leg which, while it establishes his major categories, also provides a useful means of distinguishing apoids and sphecids (Lanham 1960, and Bohart & Menke 1976:27.)

The main difficulty with the concept that bees are essentially sphecid wasps that have converted from a predatory to a pollen-gathering mode of existence is that intermediate steps have not been found either in morphology or behavior, nor do behavioral patterns of our presently living forms provide material for demonstrating transition stages. If, on the other hand one takes, as a heuristic device, the theory that bees are closely related to ants, then a multitude of possibilities are opened up. Also, one is led into new ways of looking into problems of morphology or behavior. It is not the purpose of this paper to outline a route or routes by which a bee-ant transition could be made, but rather to look at a morphological character whose distribution among the major higher groups of Hymenoptera has been neglected, namely the compound hairs which are generally thought to be characteristic only of the Apoidea (Saunders 1880:202, and most modern textbooks).

All adult bees that I have examined carefully possess at least a few compound (branched, or denticulate) hairs. Bees have in addition other types of complex hairs, such as the spirally twisted hairs in the pollen-transporting brush of the megachilids, or the spatulate hairs on the abdominal terga of some anthophorids, for example *Svastra*.

Rayment (1935:251) notes that compound hairs are present in mutillids, and Brothers (1975:495) assigns the additional "scolioid" families Eotillidae, Typhoctidae and Anthoboscidae to the list of aculeates with such hairs.

Brothers, on the basis of his sample of the ants, assigned to the formicids the character state "simple hairs." It was news to me to find that it has long been known to myrmecologists that adult ants possess complex hair types, including compound hairs. Creighton's key (1950) to North American ants mentions *Acanthomyops plumipilosis* and a species of *Triglyphothrix* as having branched hairs. In a key to the genera of ants of the world Wheeler (1922) mentions a variety of hair types in adult ants: clavate, spatulate, hooked, and denticulate (in mellitology, the last would be called obscurely compound). Ants with these hairs appear to represent scattered species or genera.

If one takes a larger view of the ants, taking into account the larvae, then the ants are not far behind the bees in having bizarre hair structure. About 90% of the genera of ants have quite hairy larvae (nearly all other aculeates have larvae with at best a few bristles). G. C. and J. Wheeler (1976) classify the hairs in nearly 30 categories, using such terms as denticulate, uncinate, anchor-shaped, branched, bifid, or clawlike. In this array, 20 types are compound, in the terminology of bee taxonomy. Data are not presented in such a way as to make a good estimate, but perhaps half the genera of ants, including at least some species of the primitive Australian *Myrmecia*, have larvae with compound hairs.

The Wheelers regard these elaborate larval hairs as adaptations for life in a communal chamber, with the hairs holding them above the substrate, providing insulation and preventing desiccation by producing a dead air space, keeping the brood together by clumping, or helping the larvae cling to vertical surfaces. Probably the only other aculeate Hymenoptera with communal brood chambers (larvae not in individual cells) are a few genera of bees. The most interesting of these on theoretical grounds are the allodapine bees, which nest in hollow twigs, have hairy larvae, and in at least one species, have compound (denticulate) hairs (Michener 1977). I am aware of no speculations concerning the function of complex hair types in adult ants.

If one assumes that the presence of compound (or in broader terms, highly modified) hairs in both bees and ants indicates a close phylogenetic relationship, he is of course faced with the difficulty that in ants it is mainly the larvae that have such hairs, while in bees they are found almost exclusively in the adults. One also has to make a judgment concerning the numerous, and so far as known at present, haphazard occurrence of such hairs in adult ants.

Probably the key question is this: are compound hairs easy to originate *de novo* in the evolutionary process, or does the establishment of this character require special conditions that are rarely met with.

A significant fact bearing on the question of whether complex hairs are easy to come by is that, so far as I can determine, the hairs are invaribly simple among the pompilid, vespid, sphecid, scoliid, and tiphiid wasps, which total approximately 15,000 species. Among the thousands of modes of life to be found in these wasps, one would expect that some species would encounter situations in which there would be adaptive value for compound hairs. Those of bees are of use in trapping pollen grains, although on many parts of the body they may also contribute to the density and resilience of the furry coat, affecting such properties as insulation or resistance to abrasion. Some of the vespid wasps gather pollen for their young, but none of these have compound hairs.

It will be assumed here, for purposes of discussion, that compound hairs are difficult to achieve in the evolutionary process, requiring the assembly of a large number of genes into a stable and long-lasting complex. Such complexes then come under the control of a single suppressor or switch gene. Variability of this gene is subjected to selection pressure, establishing alleles which determine whether or not the complex expresses itself, or modulating its expression with respect to body region or stage in life cycle.

Thus, the genetic aspects of our problem come down to this, that the gene complex for a given character, such as the morphology of a single-celled hair, may be multigenic, and may require a long period of time as well as long-lasting and unusually favorable environmental conditions for the assembly of this gene complex. But the addition of a suppressor (switch or control) gene can obscure this situation, making the character act in many ways as if it were based on a single gene. Without direct genetic experimentation, one can only make a judgment on the basis of the distribution of the character within the taxonomic framework. T. D. A. Cockerell early in his career published a few notes on bee phylogeny, but never pursued the matter in print. That he was long interested in basic aspects of the problem is indicated in a paper by himself and Louise Ireland (1933): ". . . there is increasing proof that the genes for many characters lie latent for long periods, so that similar structures appear in different branches of the same family or order. It may of course be debated whether these reappearances are due to entirely new developments or have a common origin somewhere else in the ancestral germ plasm, or whether they are due to a sort of orthogenesis. It is not necessary to assume that every case may be developed in the same way, but among bees, at any rate, the evidence for germinal continuity and latency seems rather convincing."

Applying the concept of latency to the present problem, one could speculate that the sphecids and other groups without compound hairs have an evolutionary background without gene complexes for such structures, and that favorable circumstances for their establishment never arose. The ants and bees both have a background that did include such complexes for producing varied hair types. If one assumes that the modulating capabilities of the suppressor gene make it possible to transfer the expression from larval to adult stage, or adult to larval, there is considerable room for speculative maneuver. Adult ants would be widely infiltrated with suppressed genetic complexes for varied hair types, which surface only here and there, while expression is characteristic of most larvae. In bees the situation is the other way around, with apparently all adults expressing the character, even if only in very rudimentary form. The allodapine bees, which have hairy larvae, are probably still too poorly known to make any judgement as to the extent to which complex hair types are present.

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University of Colorado Museum, Boulder, Colorado 80309.

Received for publication 23 October 1978.